BOOK REVIEW

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The Insect Societies by Edward O. Wilson. 1971. xii + 548p., $20.00. Belknap Press of Harvard University Press, 79 Garden St., Cambridge, Mass. 02138.

It is difficult to find new superlatives for a book which has received such excellent reviews, (i.e. Eberhard 1972, Richards 1971). I think it is one of the best books written in recent years in all of biology; certainly the best that has been written on social insects. One can admire and use a book even if one does not agree with every position taken by its author.

After 2 introductory chapters in which Wilson defines social behavior and states his theme of expressing insect sociology as population biology, he then presents 5 chapters to introduce some of the varieties of habits of the social wasps, the ants, the social bees, the termites, and finally the presocial insects. These introductions to the various groups of social insects are not exhaustive; rather carefully selected examples are given to illustrate major adaptive trends. Almost any of these chapters could be expanded into a book of its own.

Coleopterists will be especially interested in the chapter on presocial insects because of the good review of subsocial behavior in the beetle families, Staphylinidae, Silphidae, Hydrophilidae, Scarabaeidae, Passalidae, Tenebrionidae, Chrysomelidae, Scolytidae, and Platypodidae.

The 3 chapters on caste determination provide very good summaries of what is known about the subject in the principle groups of social insects. Furthermore, Wilson points out many of the areas where our knowledge is weak. These chapters should provide a gold mine of significant problems for future researchers.

The general area of communication is divided into 3 chapters entitled: (1) alarm and assembly, (2) recruitment, and (3) recognition, food exchange, and grooming. Under alarm and assembly, the exciting and fast moving field of social pheromones is reviewed. Tactile and auditory alarm signals are given their due also, even though Wilson believes these to be of far less significance than chemical signals. Recruitment communication is also largely olfactory, ranging from the odor of food taken back to the nests to the well known odor trails laid by ants, bees, and termites. The bee dances, which also function to recruit workers to food, are thoroughly reviewed from the points of view of their evolutionary origin, information content, and racial and species differences. Discussions of olfactory and tactile responses involved in colony recognition, caste recognition, recognition and transport of the dead, cannibalism and trophic eggs, and trophallaxis, as well as grooming and chain transport are lucidly done in the final chapter on communication. The grouping of these diverse phenomena under communication is in line with Wilson's idea which he states on p. 234, "The remarkable qualities of social life are mass phenomena that emerge from the integration of much simpler individual patterns by means of communication. If communication itself is first treated as a discrete phenomenon, the entire subject becomes much more readily analyzed."

Dominance hierarchies and their function in queen selection in wasps and the control of nestmates by the queen through the use of pheromones is treated in a chapter called, "Group effects and the control of nestmates." Social homeostasis is reviewed using thermo-regulation by bees, ants, and termites as examples as well as moisture regulation by ants and termites. Contrary to Wilson, I think the supraorganism concept will be used again when reductionist techniques have revealed all the integrating mechanisms that control the social responses in the various types of social insect colonies. Right now when we are all focused on narrowly defined problems, the concept is superfluous. If and when we start putting the pieces

together, we will once again need analogies to guide us even if they are "semiconscious".

Three of the most useful chapters are: 17, The Genetic Theory of Social Behavior; 18, Compromise and Optimization in Social Evolution; and 21, The Population Dynamics of Colonies. The genetic theory of social behavior as developed by W. D. Hamilton is an attempt to explain the evolution of social organization by the greater altruism that would be exhibited by sisters with a haploid father because they would share more genes (3/4) than those sisters with a diploid father (1/2). While this is speculative as Wilson admits, he marshalls the available evidence in its support and suggests areas where additional information is needed. Even if the theory is found to be true for the social Hymenoptera, its significance to other social groups may be more important if it can be shown that brother-sister matings occur more frequently in the higher termites than in free-living groups or even in the lower termites.

In "Compromise and Optimization in Social Evolution," Wilson reviews the areas of the evolution of monogyny (single queens per colony), and division of labor (called ergonomics). In this chapter, he again tries to apply optimization theory to the caste system in social insects. Many additional observations and experiments are needed to verify these theories.

The chapter on population dynamics of colonies summarizes the rapidly accumulating data on longevity and survivorship, colony growth and senescence, competition and territoriality, control of colony density and species diversity, and colonial dispersal. Among diverse phenomena documented, it is interesting to read that the most elaborate social behavior has evolved in those colonies with large numbers and which survive more than 1 year.

The chapter on symbioses among social insects reviews the fascinating subject of social parasitism in ants, wasps, bees, and termites. Wilson views the ultimate stage of social parasitism as worker-less reproductives which infest nests of other species and produce eggs which yield only new males and females. He also presents a new interpretation of the evolution of dulotic (slave making) ants which are usually closely related to their ant hosts. This explanation appears to hold for the social parasites of wasps and bees also where the social parasites are most closely related to their hosts.

Coleopterists will be especially interested in the chapter entitled, "Symbioses with Other Arthropods." After reviewing the general terminology of the field, he presents very useful charts giving the major groups of ectosymbionts of social insects with some of the pertinent references. He lists 37 families of Coleoptera which have been found in nests of social insects. He then reviews aspects of ectosymbiotic adaptations which include lighter body coloration, novel glands which produce appeasement substances among other things, and mimicry. He gives a fair review of mimicry but I find his explanation that mimicry is directed at predators outside the driver ant colony just as unconvincing as he finds the "Wasmann-Kistner" explanation (i.e. that the mimicry is directed at the ants and is used as an integrating mechanism). Strange ants are not destroyed by African driver ants whether they are from the same colony, other colonies of the same species, or even colonies of different species. Odor does play a role, but not a crucial one, in the driver ant's acceptance of a strange ant. If a worker ant is introduced into a raiding column from another species of driver ant colony, this creates a severe disturbance with worker ants spreading out in a circle around the point of introduction. The introduced ant reacts to this excitement by spreading its legs widely and remaining motionless with its body close to the ground. In our field work, we referred to this as "hugging the ground." After 10-15 minutes, the excitement subsides with the workers that formerly spread out returning to the columns and going about their normal raiding behavior. After this occurs, the introduced ant joins the colony in the raiding process unharmed. If the ant is of another species (*Crematogaster*), it creates still more excitement (i.e. the circle of ants running about the point of introduction is larger). It will also remain motionless until the activity returns

to normal whereupon it will remove itself from the column, again unharmed. This sort of non-aggression toward ants permits side by side raiding of *Dorylus* (*Anomma*) *nigricans* ssp. *burmeisteri* var. *molestus* (Gerst.) Mayr and *D.* (*D.*) *helvolus* Linn. It also permits easy raiding on *D.* (*A.*) *nigricans* ssp. *arcens* by *D.* (*Typhlopone*) *fulvus* ssp. *badius* var. *obscurior* Santschi—a species which is specially adapted for these kinds of raids. This may also be the reason why so many independent invasions of their colonies have occurred by so many insect species.

The Wasmann-Wilson explanation that the physogastry of the Termitoxeniinae represents a means to project fatty tissue could be true of the Termitoxeniinae which lack hypodermal glands (Malin and Kistner 1971) without being true of staphylinids where large numbers of glands have been found whenever they have been sought.

Limuloid body shape was very curiously examined. Limuloid species of myrmecophiles are at least as plentiful in the colonies of African driver ants as mimics. One wonders how predators would react to large lumbering forms in the columns, such as *Mimocete* sp., if they have exerted enough influence to cause the evolution of mimicry by other inhabitants of the same nests. In any event, no one has demonstrated yet that there are predators sitting by the side of the columns which are eating anything other than ants. The birds which are associated with Neotropical and Ethiopian army ants eat insects which are displaced by the ants, or the ants themselves, not the myrmecophiles in the columns, (Bequaert 1922:314).

The review of integrative behavior is one of the best I have ever read. Ectosymbionts have been shown to follow the chemical trails of ants, they can produce appeasement substances, can beg for food which is provided by regurgitation, can perhaps acquire their hosts odors by active grooming and/or by the production of similar or identical pheromones.

In a scant 36 pages it is hard to do justice to the tremendous array of myrmecophiles and termitophiles but Wilson even manages to include the trophobionts (Homoptera and certain Lycaenid butterflies) and speculations of why wasps and bees have fewer guests. On the whole it is a fair and creditable review; but like the ants, termites, bees, and wasps, a whole book should be devoted to it in the future.

The last chapter of the book is devoted to a brief prospectus for a unified sociobiology which accepts the validity of comparing vertebrate and insect societies if only to "increase our understanding of the unique qualities of social behavior in animals as opposed to those of man."

The technical aspects of the volume are superb. The writing is always lucid. All photographs and text drawings are superbly reproduced and no illustration was reduced to the all too frequent vanishing point merely to save space. I have looked for typographical errors and only found 1 in 548 pages (oxybeline on p. 125 should be oxyteline). Someone told me Belknap Press is a subsidized press. If so, I hope we have more of them in the future if only to preserve such fine craftsmanship.

The book is an important new textbook for courses on Social Insects. It should be read by all biologists and should provide inspirational reading to all future students of social insects who will respond to many of Wilson's positions much the way we did to those of Wheeler (1928) in his predecessor book—by further investigation.

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